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Stevenson, M. A., Mcgowan, S., Anderson, N. J., Foy, R. H., Leavitt, P. R., Mcelarney, Y. R., Engstrom, D. R., & Pla-Rabés, S. (2016). Impacts of forestry planting on primary production in upland lakes from north-west Ireland. *Global Change Biology*, *22*(4), 1490-1504. https://doi.org/10.1111/gcb.13194

Published in:
Global Change Biology

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
Link to publication record in Queen's University Belfast Research Portal

Received Date : 18-Sep-2015

Revised Date : 25-Nov-2015

Accepted Date : 04-Dec-2015

Article type : Primary Research Articles

Impacts of forestry planting on primary production in upland lakes from north-west Ireland

Running head: Algal communities in forested lakes, Ireland

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Keywords: afforestation, forest plantations, carotenoid pigments, catchment disturbance, land-use change.

Article type: Primary research article

Abstract

Planted forests are increasing in many upland regions world-wide, but knowledge about their potential effects on algal communities of catchment lakes is relatively unknown. Here the effects of afforestation were investigated using palaeolimnology at six upland lake sites in the north-west of Ireland subject to different extents of forest plantation cover (4-64% of catchment area). ^{210}Pb dated sediment cores were analysed for carotenoid pigments from algae, stable isotopes of bulk carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), and C/N ratios. In lakes with >50% of their catchment area covered by plantations, there were two- to six-fold increases in pigments from cryptophytes (alloxanthin) and significant but lower increases (39-116%) in those from colonial cyanobacteria (canthaxanthin), but no response from biomarkers of total

algal abundance (β-carotene). In contrast, lakes in catchments with <20% afforestation exhibited no consistent response to forestry practices, although all lakes exhibited fluctuations in pigments and geochemical variables due to peat cutting and upland grazing prior to forest plantation. Taken together, patterns suggest that increases in cyanobacteria and cryptophyte abundance reflect a combination of mineral and nutrient enrichment associated with forest fertilisation and organic matter influx which may have facilitated growth of mixotrophic taxa. This study demonstrates that planted forests can alter the abundance and community structure of algae in upland humic lakes of Ireland and Northern Ireland, despite long histories of prior catchment disturbance.

Introduction

Planted forests have increased substantially over the past four decades world-wide, with total planted forest area as classified by the United Nations (UN) increasing from 167.5 million hectares in 1990 to 277.9 million hectares in 2015, which accounts for 4.06% to 6.95% of total forest area (Payn *et al.*, 2015). The island of Ireland, although one of the least forested in Europe, has seen plantation forests increase from 2 to 10% of land cover, representing more than 90% of total regional forests (Forest Europe *et al.*, 2011, Department of Agriculture, 2014, Graham *et al.*, 2014). Such forestry can support rural development (McDonagh *et al.*, 2010) and offers an attractive way to sequester greenhouse gases and help offset CO_2 emissions (O'Donnell *et al.*, 2013).

Despite the ecological importance of established forests, afforestation of upland regions through ploughing, planting, fertilisation and felling can potentially impact local water bodies (Foy & Bailey-Watts, 1998, McElarney *et al.*, 2010, Woodward *et al.*, 2012, Drinan *et al.*, 2013b, Drinan *et al.*, 2013a, Dalton *et al.*, 2014, O'Driscoll *et al.*, 2016). While

widespread anthropogenic eutrophication of lowland lakes has now been demonstrated across the north temperate-subarctic (Anderson *et al.*, 2014, Taranu *et al.*, 2015), relatively less is known about how afforested lakes in smaller, upland catchments have changed in response to anthropogenic alteration of nutrient cycles. Upland lakes are subjected to multiple stressors which may alter lake ecosystem structure and function both independently and together with forestry practises (Williamson *et al.*, 2009). For example, depopulation migration (e.g., the Great Irish Famine, 1845-1850) can alter land use and lake ecosystem structure as human disturbance declines in the lowland regions (Donohue *et al.*, 2010), and habitation of upland catchments is altered. Similarly, atmospheric deposition of compounds associated with anthropogenic activities can influence upland catchments, including reactive nitrogen (Nr) (Holtgrieve *et al.*, 2011, Wolfe *et al.*, 2013), sulphuric acids, (Catalan *et al.*, 2013), phosphorus deposition (Camarero & Catalan, 2012) and pesticides (Rawn *et al.*, 2001). Finally, changes in climate teleconnection patterns such as the North Atlantic Oscillation (NAO) can alter influx of precipitation which in turn influences the input of terrestrial (dissolved organic carbon) DOC to lakes (Monteith *et al.*, 2007). Given this range of potential stressors (Maberly & Elliott, 2012), it is unclear whether upland forest plantations may exert unique measurable effects on algae even though plantation effects are possible.

Local disturbance of afforested catchments may include ploughing and planting, which together enhance the release of DOC and POC (particulate organic carbon) into lakes. These influxes may reduce light penetration and limit production (Karlsson *et al.*, 2009). Alternatively, the input of DOC may stimulate mixotrophic algae which obtain energy and nutrition both from phototrophic and phagotrophic heterotrophy (Jones, 2000, Sparber *et al.*, 2015). Influx of allochthonous materials from forestry (e.g. eroded silt) may disturb primary production by providing energy to zooplankton and consequent food-web interactions within the lake (Girvan & Foy, 2006). Further, fertilisation of coniferous plantations with

phosphorus can cause eutrophication leading to cyanobacterial blooms (Gibson, 1976). Macrophytes may decline over decades due to increased water colour following timber harvest due to soil disturbance and breakdown of brash, releasing DOC in to lakes (McElarney *et al.*, 2010). Additionally, clearcut can cause changes in physical lake mixing, with increased wind access to lake surfaces altering thermal regimes, water column mixing and deep-water oxygen status (Scully *et al.*, 2000). In principle, shifts in treeline position can also influence nitrogen availability in lakes (Bunting *et al.*, 2010), while terrestrial subsidies of allochthonous carbon to lakes can have wide-reaching trophic effects in lentic ecosystems (Cole *et al.*, 2011). However, despite clear effects of forest planting, felling and fertilisation on lake biogeochemistry, little is known of how primary producer communities have been altered in upland lakes. Such effects in landscapes where lakes are abundant, as in Ireland, have the potential to influence regional carbon fluxes (Cole *et al.*, 2007).

To explore how forestry plantations might influence upland lake ecology, we compared records of forest planting, felling and extent of forest cover with changes in pigment biomarkers (carotenoids) from algae and cyanobacteria, as well as geochemical proxies of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) cycling over the past ~150 years in dated sediment cores from six upland lakes spanning a gradient of forestry cover (4-64% of catchment afforested). The main aim was to investigate if planting, felling and percentage forest cover caused significant changes in algal abundance and community composition. We hypothesised that physical and chemical changes caused by high cover of managed forests would overwhelm other local and regional drivers and lead to changes in algal production and community composition. Specifically, we predicted that afforestation would increase algal abundance following forest fertiliser application, or decrease algal abundance due to light limiting DOC. Alternatively, we predicted that increases in DOC could favour mixotrophic taxa (e.g. cryptophytes).

Materials and Methods

Study area and forestry records

The study region is located in upland moorland areas in the north-west of Ireland across the Republic of Ireland (ROI) and Northern Ireland (NI), which together have a temperate, oceanic climate that has allowed extensive areas of blanket bog to develop (Figure 1). Commercial forest plantations represent the second largest land-use class in the NI region (McElarney *et al.*, 2010) and mostly consist of non-native Sitka spruce (*Picea sitchensis*), Lodgepole pine (*Pinus contorta spp.*) and Norway spruce (*Picea abies)* planted on areas of marginal use for agriculture referred to as rough grazing.

Six upland lakes were selected across a gradient of planted maximum forest cover ranging from 4-64% of total catchment area (Tables 1, 2) (Foy & Bailey-Watts, 1998, McElarney *et al.*, 2009, McElarney & Rippey, 2009, McElarney *et al.*, 2010). Lake elevations ranged from 83-183 m a.s.l. (Table 1), while the dominant non forest land-uses were peatland and semi-natural moorland (Table 2). Natural woodland, scrub and an additional small lake was also present in the Fadd catchment, and a small area of pasture was present in Anarry, Carrownabanny and Fadd (Table 2). Generally, the catchments were not populated, with the exception of Carrownabanny and Fadd which have a few rural houses (Table 2). Lake size ranged between 4 and 78 ha, maximum depths varied from 5.5 to 17.9 m; underlying geologies were variable (granite, quartzite, gneiss, schists limestone, shales/sandstone) and catchment soils included peat, humic or gley types (Table 1). Previous water chemistry analyses indicated a range of nutrient conditions (total phosphorus, TP 10.8-65.5 µg L^{-1} and total oxidised nitrogen, TON 0.1-1.1 mgL^{-1}), but all had relatively low phytoplankton biomass (chlorophyll *a* 2.7-9.1 µg L^{-1}), high dissolved organic carbon (DOC) concentrations 8-16.1 mg C L^{-1} and circumneutral pH from 6.3-7.9 (Table 1).

The coniferous forests of the study lakes were planted on upland areas of marginal agricultural value, exhibiting predominantly peaty organic soils and heath moorland vegetation (*Calluna, Erica, Molinia, Nardus spp.*). Previous land-use was constrained to low stocks of mostly sheep (Renou & Farrell, 2005). Consequently, we expected the disturbances associated with forest planting and felling to be distinct from those in local lowland regions where eutrophication is more common (Reynolds & Petersen, 2000) due to high levels of agriculture (Anderson, 1997). Specifically, planting of forests since the 1950s on upland uncultivated soils such as infertile blanket peats required ploughing, planting and application of fertilisers (Nieuwenhuis *et al.*, 2007). However the inability of organic soils to adsorb phosphorus (P) meant fertilisation led to higher P losses into local catchment lakes in upland lakes in NI when compared with Scottish lakes, particularly if catchments were afforested (Foy & Bailey-Watts, 1998). Since the 1990s, harvesting of trees in Ireland has increased exponentially (Department of Agriculture, 2014) with conifer harvesting followed by exceptionally high concentrations of P, nitrogen (N) and (DOC) in drainage water, probably reflecting the breakdown of brash which is left on site as a nutrient source for replanting (Cummins & Farrell, 2003a, Cummins & Farrell, 2003b, Rodgers *et al.*, 2010, Rodgers *et al.*, 2011). While in lowlands, agricultural applications of manure or nutrient fertilisers (N, P) generally occur each year, upland Irish forestry tends to apply only P fertilisers at the time of planting with the initial N requirements provided by mineralisation of soil N stimulated by ploughing and precipitation inputs (Miller, 1981). In the studied lake catchments, fertiliser N was not applied until after the forest canopy had closed, usually 12+ years after planting with the precise time interval being operationally determined and influenced by the N content of the soil. Nitrogen was applied from the air typically as urea pellets. Although the closed canopy and high biomass of trees exert a high demand for N, direct contamination of surface waters within the forested area can occur (Gibson, 1976).

Catchment forestry records were compiled from archives at the Northern Ireland Forest Service (Crockacleaven, Fadd), Coillte Teoranta Ireland Forestry (Anarry, Carrownabanny, Afurnagh) and from a study by Sweeney (2007) (Lettercraffroe). Due to the complex nature of forestry in these catchments, only the first year of tree plant and harvest (felling) at each site could be reliably identified. Relative maximum (%) catchment land cover as forest plantation (4-64%) and catchment to lake area ratios (3:1 to 15:1) were estimated by tracing land-use using data from McElarney *et al.* (2010), aerial imagery (Environmental Protection Agency, 2012), historical mapping to assess land cover in ~1880 prior to forestry activities and other land use (dating to the late 1800s) provided by the Ordnance Survey Ireland. Additionally, where we had local first-hand knowledge of past plantations that had not been accurately recorded in the archives (e.g. Fadd & Anarry), we were able to make adjustments accordingly. Four catchments were planted in the 1960s (Lettercraffroe, Crockacleaven, Anarry and Carrownabanny), and two catchments were afforested in the 1990s (Afurnagh and Fadd). The Anarry and Crockacleaven catchments were the first to be felled (in 1991), with later felling at Lettercraffroe (in 2002) and Crockacleaven (in 2007). Post-1990 catchment plantations surrounding Afurnagh and Fadd had not been felled prior to sediment coring. The catchment surrounding Fadd previously had a small area of non-native forestry (included in the 6% afforested maximum land cover) planted in the late 1970s but the young trees had been burnt prior to 1985 (field observation). This small area was confirmed as previously being moorland using historical mapping dating from the 1860s and some remnant isolated trees that survived the fire remain as evidence of the past small plantation.

Sediment coring

HON-Kajak corers (Renberg, 1991) were used to obtain a continuous sediment sequence (30-40 cm) from the deepest part of each lake during June to August 2007. All cores had a visible and undisturbed water-sediment interface and were sectioned at 1-cm intervals, except for Anarry sediments which were sectioned at 0.5-cm resolution. Subsamples were stored either frozen at -20°C for fossil pigment analyses or refrigerated for the remaining analyses.

Sediment chronology

Freeze-dried sediments from all cores were dated using ^{210}Pb, with additional samples from Afurnagh analysed for ^{137}Cs. ^{210}Pb was measured by isotope-dilution alpha spectrometry on an array of EG&G Nuclear Octête PCs, while ^{137}Cs was measured by gamma spectrometry using EG&G germanium-crystal photon (well) detectors coupled to digital gamma-ray spectrometers. Supported ^{210}Pb in each core was established from the asymptote of total ^{210}Pb at depth (below the ^{210}Pb dating horizon) or by gamma assay of ^{214}Pb in cores where supported values might be expected to vary owing to large changes in sediment lithology (Loss on Ignition, LOI). Sediment chronologies were calculated using the constant rate of supply (CRS) model with dating uncertainty estimated by first-order error propagation (Binford, 1990, Appleby, 2001). The ^{210}Pb profile for Afurnagh was spliced between two cores (collected in 2006 and 2007), as the original core did not quite reach the ^{210}Pb dating horizon, and the dating model was fitted to the ^{137}Cs peaks for 1963 and 1986 (Chernobyl). For cores where samples extended beyond the ^{210}Pb dating horizon, dates were extrapolated from the lowermost two intervals with measurable excess ^{210}Pb, which was more appropriate than spline methods given the large changes in sediment accumulation found in all cores. Dating results should therefore be considered only indicative prior to ~1820, with

results before this included to highlight pre-catchment disturbance. Dating results are presented in McElarney *et al.* (2009), however since initial dating was published, amendments to the Afurnagh model were made as additional samples for ^{137}Cs were analysed. Dating was conducted at St. Croix Watershed Research Station, Minnesota.

Pigment analysis

Chlorophyll and carotenoid pigments were analysed using an Agilent 1200 series HPLC with quaternary pump, autosampler, ODS Hypersil column (250 x 4.6 mm; 5µm particle size), and photo-diode array detector as described in Leavitt and Hodgson (2001) with the separation conditions as modified by Chen *et al.* (2001) and McGowan *et al.* (2012). Pigments were calibrated using authentic standards (DHI, Denmark) and are expressed in nmoles pigment g^{-1} organic matter, where the organic fraction was determined using weight-loss-on-ignition (LOI) at 550ºC (Heiri *et al.*, 2001). Where present, the ultra-violet radiation-(UVR-) absorbing pigment (scytonemin derivative) identified in Leavitt *et al.* (1997) was divided by the sum of key carotenoids diatoxanthin, lutein-zeaxanthin and alloxanthin and multiplied by 100 to derive a UVR index. Calibration in whole-lake experiments reveal that this index increases as a linear function of depth of UVR penetration, such that higher values indicate greater exposure to potentially-damaging UVR (Leavitt *et al.*, 1997).

Stable isotope and elemental analysis

Bulk non-acidified total carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes and elemental % C and N measurements (for C/N ratios) were analysed using a ThermoQuest (F-MAT) Delta^{PLUS}XL mass spectrometer coupled to a Carlo Erba elemental analyser and following Savage *et al.* (2004). Isotopic ratios are expressed as per mille (‰) deviation from atmospheric N_2 and organic V-PDB carbon standards, to a sample reproducibility of <0.3‰. A correction was made for the Suess effect following Schelske and Hodell (1995) by

subtracting recorded $\delta^{13}C$ values of atmospheric CO_2 from the average pre-industrial value (−6.49‰) for each sample based on its ^{210}Pb year according to the updated equation in Verburg (2007).

Statistical analysis

Historical changes in gross algal community composition were estimated using biomarker carotenoids including those from siliceous algae (diatoxanthin), cryptophytes (alloxanthin), cyanobacteria (canthaxanthin) and all algae (β-carotene). Differences between mean pigment concentrations in the pre- and post- planting periods were assessed using the non-parametric Mann-Whitney U test in SPSS (v22), as pigment data did not conform to a normal distribution. Timing of historical changes in potentially mixotrophic flagellates (alloxanthin, cryptophytes), blooming-forming taxa (canthaxanthin, cyanobacteria), diatoms (diatoxanthin), all algae (β-carotene), carbon and nitrogen stable isotopes ($\delta^{13}C$ & $\delta^{15}N$), carbon content (%C) and C/N ratios were determined for all sites with breakpoint analysis using two segment piecewise linear regression (Toms & Lesperance, 2003) in the R package 'segmented' (Muggeo, 2008). The age of first tree planting was used to train the model and included dates for Lettercraffroe (1960), Crockacleaven (1967), Anarry (1963), Carrownabanny (1960), Afurnagh (1996) and Fadd lakes (1998). Ordinary least-squares regression and two-segment piecewise linear regression (broken-stick model) was compared using analysis of variance (ANOVA) to test if the breakpoint was significant. When significant the breakpoint and its 95% upper and lower confidence intervals were plotted against age. To explore how lake response varied with the extent of forestry, pigment ratios of post-plant: pre-plant concentrations were estimated for both mean and maximum values and were plotted against percentage catchment area planted with forests. To identify regional temporal patterns, synchrony analysis (mean pairwise Pearson correlation coefficients (r)

from all possible core combinations, *S*) was performed on polynomial spline smoothed nitrogen isotope ($\delta^{15}N$) data interpolated at yearly intervals, for all lakes which were individually Z-transformed and plotted against date (Patoine & Leavitt, 2006, Vogt *et al.*, 2011).

Results

Pigments

Concentrations of sedimentary alloxanthin (cryptophytes) and canthaxanthin (cyanobacteria) increased significantly in the three lakes with the largest forest cover after planting; Crockacleaven, Lettercraffroe and Anarry (Fig. 2, 3a-c). There was a six-fold increase in cryptophyte pigments (alloxanthin) ($U=4$, $p<0.001$) in Lettercraffroe, a four-fold increase ($U=38$, $p<0.001$) in Crockacleaven, and a two-fold ($U=33$, $P<0.001$) increase at Anarry following forest planting. Canthaxanthin concentrations also increased significantly in these three lakes (U= range 0-83.5, $p<$ 0.038-0.001), but their increases were quantitatively less pronounced (39-116%) (Table 3). Ratios of maximum post-plant: pre-plant pigment concentration were significantly correlated with the extent of catchment planting for both alloxanthin (R^2-adj = 0.49, $p<0.05$) and canthaxanthin (R^2-adj = 0.62, $p<0.05$), although the proportional increase was most evident at >50% of catchment planted (Fig. 2).

Breakpoint analysis confirmed that fossil alloxanthin concentrations changed in the three lakes with the most intense forestry close to the timing of forest planting: Lettercraffroe in 1964 (95% confidence interval (CI), 1962-1966), immediately after the 1960 planting (R^2-adj = 0.97; $F = 447.92$; $p<0.001$), Crockacleaven in 1973 (95% CI 1969-1976) after 1967 planting (R^2-adj = 0.93; $F = 133.14$; $p<0.001$), and Anarry in 1961 (95% CI 1945-1977)

which was close to 1963 planting (R^2-adj = 0.76, F = 14.5, p<0.001) (Fig. 3, S. Table 1). In contrast, the breakpoints for canthaxanthin increases were less clear cut with wide confidence limits and therefore not so closely aligned to the commencement of afforestation. The breakpoint occurred at 1942 in Lettercraffroe (95% CI 1924-1960) compared to tree planting starting in 1960 although the 95% CI of 1924-1960 just encompasses the start of planting (R^2-adj = 0.43; F = 14.86, p<0.001). In Crockacleaven the canthaxanthin breakpoint in 1977 was after the 1967 planting date although again the 95% CI of the breakpoint 1967-1987 just overlaps with the planting year after 1967 planting R^2-adj = 0.63; F=20.13; p<0.001. In Anarry there was initially no agreement with planting as the breakpoint for canthaxanthin was not until 2001 (95% CI 1994-2007), which was coincident with felling and well after the first planting of 1963 (R^2-adj = 0.87, F = 4.4, p<0.05) (Fig. 3, S. Table 1). However, there was agreement when recent post-fell samples were removed from the model resulting in a breakpoint of 1962 (95% CI 1947-1977) close to 1963 planting (R^2-adj = 0.90; F = 11.33). Interestingly, total algal abundance as β-carotene exhibited no clear relationship with forest planting in these three heavily impacted catchments (Fig. 3a-c), while UVR pigments were absent from Crockacleaven or Lettercraffroe (Fig. 2a,b), but increased in Anarry sediments after ~1800 until the initial forestry planting (Fig. 3c).

Algal communities were less significantly affected by catchment afforestation in the three remaining lakes where forest plantations accounted for <20% of catchment area (Fig. 3d-f). Carrownabanny, Fadd and Afurnagh all featured variable pigment profiles and UVR indices both before and after forest planting (Fig 3d-f). Unlike the more heavily managed catchments, fossil alloxanthin or canthaxanthin content exhibited little directional change in Carrownabanny and planting was too recent in control sites Fadd and Afurnagh to test for the effect of planting. In general, breakpoints for alloxanthin occurred slightly after the onset of forest planting in Carrownabanny and Afurnagh, but in Fadd the breakpoint was not

significant (Fig. 3d-f, S. Table 2). Although there was a breakpoint relationship between diatoxanthin (diatoms), canthaxanthin (cryptophytes) and β-carotene (total algae) and plant date in Afurnagh, the concentrations were highly variable before planting, suggesting that changes of similar magnitude to forestry had precedent in the past (Fig. 3f, S. Table 2).

Fossil pigment concentrations varied considerably through time in most lakes prior to forest planting within the 20th century (Fig. 3). For example, in Lettercraffroe, there was a gradual decline in diatoxanthin (diatoms) from ~1700 to ~2000, with pulses of β-carotene (total algae) throughout the 1700s and ~1900 (Fig 3b). In contrast, Crockacleaven exhibited contemporaneous peaks of diatoxanthin (mainly diatoms) and β-carotene between ~1900 and ~1950 (Fig. 3a), whereas Anarry featured a gradual increase in all pigments from the start of the record prior to 1963 planting (Fig. 3c). Fossil pigments in Carrownabanny and Afurnagh fluctuated considerably throughout their records (Fig. 3d,e) with marked declines in Fadd between ~1860 and ~1910 followed by an increase in alloxanthin pigment peaking around ~1940 (Fig. 3f).

Geochemistry

Geochemical and isotopic proxies suggest that afforestation resulted in changes in the character and provenance of sedimentary carbon in lakes with greatest forest cover (Fig. 4). For example, sedimentary C/N ratios declined following initial tree planting in lakes with >50% of catchment forest cover (Fig. 4a-c), while trends were less marked in Fadd (4e) (6% afforestation) and declined before planting in Anarry (57% afforestation) and Afurnagh (4% afforestation) (Fig. 4c, f). In contrast, $\delta^{13}C$ values increased in all lakes after plantations were established, except intensively forested Lettercraffroe where sedimentary carbon isotope ratios were sharply depleted after planting (Fig. 4b). At Lettercraffroe breakpoints for $\delta^{13}C$ ratios (1962, 95% CI 1957-1967), $\delta^{15}N$ (1961, 95% CI 1954-1967) and C/N ratios (1965, CI

1958-1971) were all clearly coincident with tree planting (all $p<0.001$) (Fig. 4b, S. Table 1). However, in Crockacleaven no breakpoints were perfectly coincident with planting; rather the breakpoint for C/N was slightly after planting (1980, 95% CI 1974-1985), while in Anarry only the breakpoint for $\delta^{13}C$ was coincident with forestry (1972, 95% CI 1950-1993) (Fig. 4a,c; S. Table 2). When plotted together (Fig. 5), lake zones defined by C/N ratios and $\delta^{13}C$ values revealed that afforestation typically produced changes characteristic of increased algal production in dilute lakes (lower C/N, enriched $\delta^{13}C$), with the exception of Lettercraffroe (lower C/N but depleted $\delta^{13}C$ (Fig. 4b)) and Fadd for which there were no separation of pre and post planting samples.

Overall, nitrogen isotope values declined during the 20th century, with relatively high rates of depletion being recorded in many sites after ca. 1950 (Fig. 4 & 6). In the case of Lettercraffroe, Anarry, and Carrownabanny, $\delta^{15}N$ declined during forest planting; however, while Crockacleaven and Fadd exhibited few pronounced changes, declines at Afurnagh clearly preceded forest planting. The declines in $\delta^{15}N$ were found to be highly synchronous in Afurnagh, Lettercraffroe, Carrownabanny, Anarry and Fadd (S =0.94, $p<0.001$), and to a lesser extent when Crockacleaven was included in the model (S=0.58, $p<0.001$) (Fig. 6). When ratios of mean and maximum post-plant: pre-plant $\delta^{15}N$ were plotted against percentage forestry, a clear trend was established between higher planted forestry and $\delta^{15}N$ (maximum R^2-adj = 0.64, $p<0.03$) (S. Fig. 2).

Geochemical and isotopic parameters also exhibited high temporal variability prior to forest planting. For example, in Anarry, carbon content varied between ~29% and 20% throughout the record, whereas analysis of sediments from Carrownabanny and Afurnagh recorded a decline in C content prior to the planting of the forests (Fig. 4c,d,f). Similarly, C/N ratios declined and $\delta^{13}C$ values increased in Anarry, Carrownabanny and Afurnagh well before planting (Fig. 4c,d,f). Across Carrownabanny, Fadd and Afurnagh, no breakpoints

were coincident with planting and only the change in $\delta^{13}C$ in Carrownabanny was coincident with felling (1998, 95% CI 1978-1998) (Fig. 4d-f; S. Table 2). In Fadd, a sharp decline in carbon content, C/N ratios and an increase in $\delta^{13}C$ values occurred ~1890, followed by a return to previous levels by ~1940 (Fig. 4e). Similarly, temporal variation in $\delta^{13}C$ and $\delta^{15}N$ values was generally lower in the 19th century than during the 20th century.

Discussion

In lakes where forestry exceeded 50% of the catchment land cover, the timing of algal community change is consistent with the hypothesis that forest plantations had a significant impact on algal abundance and gross community composition. In particular, cryptophytes (as alloxanthin) and to a lesser extent colonial cyanobacteria (as canthaxanthin) increased as a function of the percentage of afforestation in the lake catchment (Figure 2). In contrast, we found little evidence of forestry impacts in lakes with lower forest cover (<20%), although all sites exhibited substantial and individualistic variability in pigment and isotopic records prior to initiation of conifer plantations. Together, these findings suggest that water quality in upland lakes can be threatened by catchment forestry if planting represents more than half of the catchment area.

Limnological consequences of intensive conifer plantations

The significant increases in concentrations of fossil canthaxanthin and alloxanthin after tree planting in Crockacleaven, Lettercraffroe and, to a lesser extent, Anarry catchments suggest that forest planting was a major factor regulating growth of cryptophytes and cyanobacteria in these lakes (Fig. 3). Consistent with this interpretation, C/N ratios declined in these lakes immediately after forest planting indicating that more of the sedimentary

carbon was derived from algal sources (Meyers & Teranes, 2001), while in most cases $\delta^{13}C$ values increased <1‰ from depleted values between −28 and −30‰. In most lakes with enrichment, this meant $\delta^{13}C$ isotopes moved to values characteristic of algal respired CO_2 (ca. −27‰) (Meyers & Teranes, 2001). However, in Lettercraffroe there was a decline in $\delta^{13}C$ after planting as previous values were higher, indicating a switch in algal source (Figure 5).

Management of afforested catchments may favour enhanced algal abundance through runoff of fertilisers. Commercial forestry in ROI and NI has often fertilised soils at rates of 50-90 kg P/ha (Dickson & Savill, 1974) which exceed the P-binding capacity of such iron- and aluminium-poor soils (Maguire *et al.*, 2001). Disproportionate increases in cyanobacteria following elevated nutrient influx have been recorded in many regions of the northern hemisphere (Taranu *et al.* 2015), and reflect multiple concomitant fertilisation mechanisms such as deposition of atmospheric nutrients (Holtgrieve *et al.*, 2011), agriculture (Battarbee *et al.*, 2005, Bunting *et al.*, 2007, Moorhouse *et al.*, 2014), and urbanisation (Leavitt *et al.*, 2006, McGowan, 2016). Although total algal biomass usually increases with eutrophication, increases in phytoplankton production associated with fertilisation may out-compete benthic algae, and compress the photic zone in the water column, leading to changes in overall algal habitat and community composition (McGowan *et al.*, 2005). Although speculative, we infer that such shifts may underlie the observation that sharp increases in cryptophytes and cyanobacterial abundance after forest planting was not marked by a concomitant increase in total algal deposition (as β-carotene).

Forestry planting and felling may have also favoured development of mixotrophic populations by increasing influx of terrestrial organic matter to upland lakes through several mechanisms (Jansson *et al.*, 2000, Jansson *et al.*, 2001). In general, forestry planting and felling may increase the export of dissolved organic matter (DOM) and dissolved organic carbon (DOC) to lakes and streams (Carignan *et al.*, 2000, O'Driscoll *et al.*, 2006, Schelker *et*

al., 2012). First this increased influx of DOM might directly fertilise potentially mixotrophic algae such as cryptophytes and cyanobacteria (Jones, 2000, Burkholder *et al.*, 2008). Second, elevated DOM and particular organic matter (POM) influx can stimulate primary production indirectly by providing a substrate for heterotrophic bacteria (Tranvik, 1990) which can either be ingested by phagotrophic heterotrophs (Isaksson *et al.*, 1999, Jones, 2000) or which may provide dissolved nutrients to autotrophs after consumption by herbivores (Sanders *et al.*, 1990). Third, increased DOM influx could reduce light penetration and favour highly motile and predominantly planktonic (cryptophytes) or buoyant (colonial cyanobacteria) taxa which can better exploit shallow photic zones (Ojala *et al.*, 1996, Staehr *et al.*, 2010), compared with dinoflagellates and chrysophytes. Consistent with this last mechanism, we note that fossil diatom assemblages switch from predominantly benthic to more planktonic forms in Crockacleaven and Lettercraffroe following plantation development (McElarney *et al.*, 2009). While it is possible that precipitation-derived increases in DOC runoff may also occur in these lakes (Monteith *et al.*, 2007), the asynchronous timing of cryptophyte expansion argues against a coherent regional driver of algal community change.

Other controls of algal abundance

Upland lakes of the north west of Ireland exhibited substantial variation in algal abundance independent of the effects of catchment afforestation, likely reflecting the combined effects of regional and local factors. Among regional stressors, the island of Ireland may have been impacted by recent atmospheric warming since c. 1986 (Anderson *et al.*, 2012) and changes in hydrology associated with the NAO (George *et al.*, 2004, Adrian *et al.*, 2006), altered influx of nitrogen due to deposition of atmospheric Nr (Holtgrieve *et al.*, 2011), elevated influx of terrestrial DOM (Monteith *et al.*, 2007), or acidic precipitation and recovery (Battarbee *et al.*, 1990, Jones *et al.*, 1993, Flower *et al.*, 1994). In addition, peat extraction for fuel has been practised regionally since prehistoric times, but peaked during the

19th century population expansion, and again in the 1940s with the introduction of mechanized peat harvest (Renou & Farrell, 2005). While these factors did not obscure the effects of afforestation in catchments with >50% of land cover conversion to forests (Fig. 3a-c), such processes may have had a mediating effect on less forestry-affected sites, as well as all basins prior to, and during the advent of forest plantations.

All lakes exhibited evidence of local land-use disturbance prior to planting of forests, but such events were particularly pronounced in lakes with lower cover of coniferous trees. For example, C/N ratios slowly declined in Anarry, Carrownabanny and Afurnagh suggesting increased algal contributions before planting, while there were multiple fluctuations in all proxies in Afurnagh and Fadd. These changes likely reflect the combined impacts of upland grazing and peat cutting, rather than lowland agricultural and urbanisation factors, as these upland catchments were of rough pasture and moorland unsuitable for agriculture prior to afforestation (Renou & Farrell, 2005). Extensive upland grazing by sheep is known to have contributed to the decline of *Calluna* on the heath moorland of Ireland, elevated local soil erosion (Stevenson & Thompson, 1993), and contributed to increased sediment yields despite low sheep stocking densities (Evans, 1997). Similarly, peat cutting directly destabilises catchments, increasing sediment and nutrient runoff (Renou-Wilson & Farrell, 2007) and provides an additional mechanism to account for the perturbations across multiple proxies and sites before planting (Carrownabanny, Afurnagh and Fadd). Notable is the increase in alloxanthin pigment in Fadd prior to forestry (peaking in the 1940s), a pattern which may record increased inputs of terrestrial organic matter and, consequently, mixotrophy (Fig. 3e). Additionally, catchment to lake area ratios (Table 2) which are slightly larger in the lakes with lower percentage afforestation (Carrownabanny, Afurnagh, Fadd) may increase the potential in these lakes for non-forestry catchment disturbance events, which are usually highly localised, to be recorded.

Although acidification has been observed previously in Irish upland lakes (Flower *et al.*, 1994), we did not find consistent sedimentary evidence of the effects of regional acid deposition: algal pigment changes were either clearly concomitant to forestry, or did not exhibit a common pattern among lakes during the interval when acidification would be expected to be evident in the mid-19th century (as early as the 1860s) (Flower *et al.*, 1994, Aherne & Curtis, 2003, O'Dwyer & Taylor, 2010). Although, Crockacleaven and Lettercraffroe (pH 6.3) (Table 1) presently have a lower pH than other sites, and exhibit some evidence from fossil diatoms of recovery from acidification (N.J. Anderson, unpublished data), these chemical conditions are unlikely to be sufficiently acidified to affect gross algal community composition.

Declines in $\delta^{15}N$ in five of the six lakes were highly synchronous ($S = 0.94$, $p<0.001$) which point to broad regional drivers of change (Fig. 6). Declines were also moderately synchronous ($S = 0.58$, $p < 0.001$) if all six lakes were considered. The intensity of the North Atlantic Oscillation (George *et al.*, 2004) and the north-south movements of the Gulf Stream (Taylor, 1996) have been linked to coherent regional forcings of algae in the UK Lake District (McGowan *et al.*, 2012, Moorhouse *et al.*, 2014) and nitrate deposition in Ireland (Jennings & Allott, 2006, Anderson *et al.*, 2012). Since the breakpoint in $\delta^{15}N$ decline is only coincident with planting in one lake (Lettercraffroe) we do not interpret the broad pattern of $\delta^{15}N$ depletion to be driven by catchment land use. Instead, this highly synchronous decline in $\delta^{15}N$ may be related to atmospheric deposition of Nr (Holtgrieve *et al.*, 2011) and-or DOM-N influx associated with post-1970 changes in rainfall patterns and DOM runoff. Increased export of DOC from upland catchments in the Northern Hemisphere (Freeman *et al.*, 2001) have been associated with declines in atmospheric deposition of anthropogenic sulphur and climate mediated sea salt deposition (Monteith *et al.*, 2007). Additionally, a notable increase in DOC has been recorded in Northern Ireland upland softwater lakes

(McElarney *et al.*, 2010) so both the direct deposition of Nr and elevated DOM runoff could alter N isotope ratios. In general, these effects should be most pronounced in systems with intrinsically low N content (Holtgrieve *et al.*, 2011), or those receiving particularly high influx of Nr (Galloway *et al.*, 2008). Regardless of the precise pathway of N influx, synchronous declines in $\delta^{15}N$ during the 20th century are mostly consistent with regional mechanisms (Hu *et al.*, 2014) rather than upland forest planting and felling activities.

Recommendations for forestry management

Our study provides clear evidence that forestry planting in upland catchments leads to a major reorganization of algal communities (cryptophytes, cyanobacteria) in lakes with >50% catchment afforestation. These findings suggest that forestry managers can identify lakes likely to be impacted by plantation through a simple estimate of proportional land use. At sites where catchments are 50% planted or more, it is especially important that strategies are enacted to reduce potential damage to aquatic ecosystems, including application of discontinuous forestry, harvesting only on dry soils, maintenance of marginal buffer strips and brash-mats. Elsewhere, these procedures have been shown to most effectively reduce nutrient, soil and suspended solid loss (Giller & O'Halloran, 2004, Rodgers *et al.*, 2011, Xiao *et al.*, 2012). In Ireland upland catchment buffer strips have been confirmed to help reduce the impact on aquatic ecology (Ryder *et al.*, 2011), with a recommendation for a more targeted, species-specific fertilisation to be applied gradually near tree roots, rather than spread openly on bare soil to minimise wastage and subsequent leaching (Renou-Wilson & Farrell, 2007). The Irish Forest Service now aim to reduce fertilisation at planting to 42 kg P/ha (Cummins & Farrell, 2003b). Such activities will likely help reduce cyanobacteria blooms and toxicity in catchment lakes, helping to maintain water quality both for aquatic communities and downstream water management.

Detailed phytoplankton experimentation studies on impacted lakes may also help elucidate the role of potential cryptophyte mixotrophy in these dystrophic, anthropogenically disturbed humic forest lakes. Future research needs to better understand the mechanisms that promote mixotrophy and help guide our understanding of carbon and nutrient dynamics in impacted lakes (Jansson, 1998, Jansson *et al.*, 2000, Jones, 2000). Efforts to increase forest cover in the ROI to 17% by 2030 (Renou & Farrell, 2005) are a response to the growing need for timber and the effectiveness of afforestation to sequester carbon and meet emission reduction targets (Fuchs *et al.*, 2013, Bárcena *et al.*, 2014). However our study demonstrates for the first time for both cryptophyte and cyanobacterial algal communities together that forestry planting is capable of altering lake ecosystem structure and function. Such continuous pressure for forest management is unlikely to abate, making it increasingly important to understand how intensive management practices like upland forestry can, if improperly managed interact with regional stressors to change and modify upland aquatic ecosystems.

Acknowledgements

This work was funded by the EU INTERREG IIIA Programme, Department of Agriculture and Rural Development, (Northern Ireland), Coillte, (Republic of Ireland), Queens University Belfast, Department of Geography, Loughborough University (NJA), School of Geography, University of Nottingham (MAS & SMcG) and NSERC Canada and the Canada Research Chair program (PRL). Funding for MAS during the writing of this paper was provided by a NERC/ESRC PhD studentship (ES/J500100/1). We thank Una Hewson (Coillte) for providing forestry records for lakes in Ireland, Teresa Needham and Graham Morris for laboratory support, Björn Wissel and Zoraida Quiñones-Rivera for stable

isotope analyses and George Swann for his comments on an earlier version of this manuscript. We also thank: the staff at AFBI Belfast for assistance with water chemistry records, Louise Vaughan, Chris Barry and Katherine Webster for help and advice with compiling these records, Elaine Watts for cartographic advice, Joanna Girvan for assistance with coring and James Johnson, Zofia Taranu, and Heather Moorhouse for help and advice with the R programming language.

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List of figures

Figure 1: Location of the six study lakes selected for sediment coring.

Figure 2: Ratio of maximum post-plant pigment concentration (since first plant) over maximum pre-plant (since 1900) pigment concentration against catchment percentage planted forestry. Linear regressions are presented for alloxanthin (cryptophytes) and canthaxanthin (cyanobacteria) pigments. A similar result was obtained when mean post-plant pigment concentration over mean pre-plant pigment concentrations were used (canthaxanthin adjusted $r^2 = 0.62$, $p = 0.04$; alloxanthin adjusted $r^2 = 0.49$, $p = 0.07$) (S. Figure 1).

Figure 3: Changes in pigment concentrations for (a) Crockacleaven, (b) Lettercraffroe, (c) Anarry, (d) Carrownabanny, (e) Fadd and (f) Afurnagh. Variables include: (i) siliceous algae (diatoxanthin), (ii) cryptophytes (alloxanthin), (iii) cyanobacteria (canthaxanthin), (iv) total algae (β-carotene) and (v) water clarity inferred from the (UVR) index. Date of first planting (indicated by PLANT), and date of first felling (indicated by FELL). 95% confidence interval breakpoints highlighted (light shading = below breakpoint; dark shading = above breakpoint). Breakpoints presented where ANOVA analysis indicated the broken stick model was more appropriate than the linear model ($p<0.05$) (S. Table 1 & 2). Maximum percentage forestry is indicated at the top right hand of each sub-plot.

Figure 4: Changes in bulk and isotopic measures for (a) Crockacleaven, (b) Lettercraffroe, (c) Anarry, (d) Carrownabanny, (e) Fadd and (f) Afurnagh. Variables include: (i) carbon content determined by elemental analysis on bulk carbon (%C), (ii) C/N ratio, (iii) $\delta^{13}C$, and (iv) $\delta^{15}N$. Date of first planting (indicated by PLANT), and date of first felling (indicated by FELL). 95% confidence interval breakpoints highlighted (light shading = below breakpoint; dark shading = above breakpoint). Breakpoints presented where ANOVA analysis indicated the broken stick model was more appropriate than the linear model ($p<0.05$) (S. Table 1 & 2).

Figure 5: Plot of C/N ratio against $\delta^{13}C$ (corrected for the Suess effect) for samples from Lettercraffroe (hexagon), Crockacleaven (diamond), Anarry (upwards triangle), Carrownabanny (square), Afurnagh (circle), and Fadd (downwards triangle). Filled symbols denote sample prior to afforestation, open symbols denote after afforestation. Zones occupied by each lake are encircled to aid interpretation and brackets denote the first plant year.

Figure 6: Synchrony analysis of polynomial spline smoothed nitrogen isotope ($\delta^{15}N$) data interpolated at yearly intervals and Z-transformed against date for Afurnagh, Lettercraffroe, Anarry, Fadd and Carrownabanny, with significance established using 999 Monte Carlo randomizations. When Crockacleaven was included in the model the results indicated lower, but still significant synchrony ($S = 0.58$, $p < 0.001$).

Supporting information

1. Supporting information pack containing additional summary diagram figures (S. Fig 1 & 2) and breakpoint summary tables (S. Table 1 & 2).

Table 1: Study lakes: location, geology and water chemistry measurements.

	Crockacleaven	**Lettercraffroe**	**Anarry**	**Carrownabanny**	**Fadd**	**Afurnagh**
Latitude (N)	54°20'39.20"	53°22'50.56"	54°15'25.44"	54° 9'27.88"	54°25'28.61"	54°33'59.30"
Longitude (W)	7°15'23.53"	9°25'17.39"	8°16'34.79"	8°40'43.84"	7°52'55.63"	7°52'56.97"
Country	NI	ROI	ROI	ROI	NI	ROI
Elevation (m a.s.l)	183	163[(a)]	83	102	138	123
Lake area (ha)	4	78	12	7.2	6	7
Max depth (m)	5.5	17.9[(a)]	7.8	6.5	14.5	8.5
Water residence time (years)	0.4	0.6	0.6	0.4	0.4	0.2
Main soil types	Deep peat, humic gley	Rock outcrop, peat	Peat, gley	Gley, peaty gley (grey brown podzols)	Peat, gley	Peat, humic ranker
Bedrock geology	Sandstone, Shales, Limestone	Granite	Pre-Cambiran Quartzite, Gneisses and Schist	Pre-Cambiran Quartzite, Gneisses and Schist. Lake on sandstone.	Sandstone, shales	Pre-Cambiran Quartzite, Gneisses and Schist
Conductivity @20°C (μScm^{-1})	53.9	82.5	85.0	120.3	82.6	66.6
Alkalinity (mequiv l^{-1})	0.1	0.1	0.4	0.6	0.7	0.2
pH	6.3	6.3	6.7	7.4	7.9	7.5
SiO_2 (mg l^{-1})	1.6	0.6	1.4	0.3	0.4	1.7
TP ($\mu g\ l^{-1}$)	65.5	10.8	37.3	56	11	22.5
TON (mg l^{-1})	1.1	0.2	0.1	0.3	0.5	0.0
Chlorophyll *a* ($\mu g\ l^{-1}$)	6.0	9.1	5.0	3.1	3.4	1.4
DOC (mg l^{-1})	14	-	-	16.1	8	11.4

Water chemistry measurements complied from: McElarney *et al.* (2009) and McElarney *et al.* (2010), AFBI sampling and EPA (Ireland) sampling for Water Framework Directive compliance. [(a)] Denotes lake variables compiled from De Eyto *et al.* (2002). Abbreviations: silica (SiO_2), total phosphorus (TP), dissolved organic carbon (DOC), total oxidised nitrogen (TON). For the four lakes in the ROI catchment geology was determined using the Geological Survey of Ireland 1:10000 Bedrock Geology GIS layer while catchment soil types were based on the National Soils Map of Ireland 1:50000 Irish Forest Soils GIS layer (Fealy *et al.*, 2009). For the two lakes in NI the maps of the Northern Ireland Soil Survey (1:50000) and Geological Survey of Northern Ireland (1:63360) were used (Cruickshank, 1997).

Table 2: Study lakes afforestation and land cover compiled from forestry records, historical mapping and aerial imagery.

Lake	Crockacleaven	Lettercraffroe	Anarry	Carrownabanny	Fadd	Afurnagh
First plant (year)	1967 [(a)]	1960 [(b)]	1963 [(c)]	1960 [(c)]	1996 [(c)]	1998 [(a)]
First fell (year)	2000 [(a)]	2002 [(b)]	1991 [(c)]	1991 [(c)]	-	-
Afforested maximum land cover (%)	64	63	57	19	6	4
Catchment to lake area ratio	4:1	3:1	4:1	7:1	14:1	15:1
Catchment area (excluding lake) (ha)	16	238	53	52	82	102
Heath/moorland/bog (%)	26	37	39	70	76	96
Natural woodland & scrub (%)	0	0	0	0	8	0
Pasture (%)	10	0	4	11	2	0
Other Lakes (%)	0	0	0	0	7	0
Houses in 1860 (No.)	0	0	0	4	1	0
Houses in 2007 (No.)	0	0	0	1	1	0

Plant and fell measurements complied from: Northern Ireland Forestry Service [(a)]; Sweeney (2007) [(b)]; Coillte Teoranta Ireland Forestry [(c)]. Other values estimated based on McElarney et al. (2010), aerial imagery (Environmental Protection Agency, 2012), historical mapping provided by the Ordnance Survey Ireland and from direct observation.

Table 3: Mean concentration (±SD) and non-parametric Mann–Whitney *U* test values before and after afforestation for selected key pigment variables (diatoxanthin, alloxanthin, canthaxanthin and β-carotene).

			Crockacleaven	Lettercraffroe	Anarry	Carrownabanny	Fadd	Afurnagh
First planting			1967	1960	1963	1960	1996	1998
Diatoms (diatoxanthin)	Mean concentration (±SD)	*before*	2.1±0.69	5.4±1.6	3.3±1.35	3.5±1.43	6.5±2.36	2.2±0.85
		after	2.2±1.0	3.7±1.5	5.8±1.58	3.7±1.8	6.1±3.7	1±0.84
	U		117	73	99	121.5	32	31
	P		0.65	0.015*	<0.001**	0.768	0.822	0.005*
Cryptophytes (alloxanthin)	Mean concentration (±SD)	*before*	1.7±0.48	1.0±0.29	3.8±1.25	2.6±1.35	12.5±6.25	1.8±0.57
		after	6.8±4.1	6.8±4.7	7.9±2.1	5.0±1.9	11.8±5.4	2.1±0.9
	U		38	4	33	41	34	75
	P		<0.001**	<0.001**	<0.001**	0.001*	0.922	0.427
Filamentous cyanobacteria (canthaxanthin)	Mean concentration (±SD)	*before*	0.89±0.25	0.80±0.30	2.08±0.93	1.47±0.47	5.02±1.23	0.56±0.24
		after	1.24±0.55	1.3±0.69	4.50±0.91	1.78±0.31	6.14±1.43	0.45±0.18
	U		72	83.5	0	81.5	19	73.5
	P		0.033*	0.038*	<0.001**	0.087	0.266	0.379
All algae (β-carotene)	Mean concentration (±SD)	*before*	0.4±0.28	0.4±0.36	2.9±1.33	2.8±1.57	6.1±3.56	1.1±0.49
		after	0.4±0.32	0.1±0.08	5.4±1.56	2.3±1.28	6.4±7.57	0.2±0.32
	U		113	52	69	108	33	11
	P		0.548	0.001*	<0.001**	0.454	0.871	<0.001**
	No. samples	*before*	20	30	18	10	36	7
		after	13	10	42	26	2	27

*, $p < 0.05$; **, $p < 0.001$ All concentrations in nmol pigment g^{-1} organic weight sediment.